Cambios en la ecología trófica de los depredadores apicales del Mar Argentino durante el Holoceno

Fabiana Saporiti

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Paleoindian pinniped exploitation in South America was driven by oceanic productivity

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1. Introduction

Concern about the conservation of marine resources has increased during recent decades as evidence that human exploitation has caused major changes in most marine ecosystems has grown (Pauly et al., 1998; Jackson et al., 2001; Pauly et al., 2005). Although recent examples of fisheries recovery after collapse certainly exist (Worm et al., 2009), marine resource exploitation has increased dramatically worldwide during recent centuries (Pauly et al., 1998; Jackson et al., 2001; Pauly et al., 2005). However, the impact of other preindustrial-fished and the ecological extinction of coastal marine megafauna are thought to predate industrialized fishing in many cases.

The historical record clearly demonstrates that preindustrialized European societies overexploited coastal marine mammals (Dulvy et al., 2009) and that European settlement triggered the overexploitation of coastal marine megafauna on other continents (Jackson et al., 2001). However, the impact of other preindustrialized cultures on coastal marine resources remains contentious. An increasing number of multidisciplinary studies examining the interactions between prehistoric peoples and their environments suggest that, at least in some cases, ancient peoples caused cumulative and often irreversible impacts on natural landscapes and biotic resources worldwide (Kirch, 2005).

The study of the Holocene human settlements along the Argentine coast began after 1936, as archaeologists viewed marine resources as minor dietary sources for local hunter-gatherers, who were considered primarily terrestrial (Orquera and Gómez Otero, 2007). Only since the 1980s, with the improvement of archaeological methods and based on the productivity of the seas and the

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high nutritional value of some marine species, was the importance of such resources recognized (Gómez Otero, 2006, 2007; Orquera and Gómez Otero, 2007; Moreno, 2008).

Available evidence indicates that the southern end of South America was colonized more than 12,000 years ago by humans dispersing along the Pacific coastline of the Americas (Miotti et al., 2003; Dillehay et al., 2008; McKeechnie and Wigen, 2011; Moss and Losey, 2011; Orquera et al., 2011). These humans possessed the technology to use marine resources, notably fish, birds, and molluscs (Keeler et al., 1998; Dillehay et al., 2008; Betts et al., 2011; Erlanson et al., 2011; Gifford-Gonzalez, 2011), but intense exploitation did not develop until much later, in the Middle Holocene, probably as a consequence of a technological improvement (Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011).

However, the hypothesis that human occupation was earlier than currently thought, especially in certain sectors of the coast where the bathymetry is particularly smooth (Ponce et al., 2011), is still open (Gómez Otero, 2006).

Pinnipeds were especially important prey for both the hunter-gatherers inhabiting the Beagle Channel and the southern coast of Chile, who based their living on marine resources (Schiaivini, 1993; Orquera and Piana, 1999; Yesner et al., 2003; Orquera et al., 2011; Tivoli and Zangrando, 2011, 2012) who inhabited central and northern Patagonia, only partially dependent on terrestrial resources (Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009). According to the zooarchaeological record, the human populations inhabiting the Beagle Channel approximately 6000 BP were highly reliant on marine resources, mainly fur seals (Arctocephalus australis) which were the main source of food and raw material for many millennia (Orquera and Piana, 1999; Orquera et al., 2011; Tivoli and Zangrando, 2011). Conversely, people inhabiting northern and central Patagonia exploited both terrestrial and marine resources, but the exploitation of pinnipeds, especially sea lions (Otaria flavescens), developed approximately 3000 BP, when seasonal settlements were established close to sea lion rookeries (Gómez Otero, 2006; Favier Dubois et al., 2009). Sea lion exploitation was intense in the northern province of Rio Negro from 3100 to 2200 BP and was followed by a period of moderate exploitation from 1500 to 420 BP (Favier Dubois et al., 2009). In contrast, sea lion exploitation in Chubut province was moderate from 3000 to 1000 BP, and intensified from 1000 to 350 BP (Gómez Otero, 2006, 2007).

Although both groups of hunter-gatherers differed dramatically in technology and in historical patterns of resource exploitation (Orquera and Piana, 1999; Orquera and Gómez Otero, 2007; Moreno, 2008; Orquera et al., 2011), everywhere the zooarchaeological record reveals a general decline in the consumption of pinnipeds after several centuries of exploitation (Yesner et al., 2003; Gómez Otero, 2007; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). Similar declines in the use of pinnipeds by maritime hunter-gatherers in the north Pacific have been on occasions linked to increasing sea surface temperature (Colten and Arnold, 1998; Betts et al., 2011), but most often to over-exploitation by humans in the absence of strong evidence supporting climate forcing (Porcasi et al., 2000; Lyman, 2003; Jones et al., 2004; Newsome et al., 2007). Over-exploitation has also been suggested as the reason for the progressive decline in the presence of fur seals in the zooarchaeological record from the Beagle Channel (Orquera et al., 2011; Tivoli and Zangrando, 2011), as the pollen record (Heusser, 1980) and the stable oxygen isotopes (Olbrich et al., 1998; Saporiti et al., 2012) suggested no relationship between climate patterns and resources used by hunter-gatherers during the second half of the Holocene. However, nothing is known about how marine productivity varied throughout that period, a critical point because dense populations of sea lions and fur seals only thrive in highly productive environments (Bowen et al., 2008).

Primary productivity in coastal areas usually depends on nitrogen availability, which increases due to high freshwater runoff, intense vertical mixing and deep water upwelling (Gruber, 2008). All these processes also promote nitrogen recycling over nitrogen fixation and hence modify the relative abundance of heavy isotopes of nitrogen (15N) in the tissues of aquatic primary producers (Calvert et al., 1992; Wu et al., 1997; Waser et al., 2000). As stable isotope ratios in prey are transferred to their predators, δ15N values in herbivorous molluscs are expected to reveal δ15N values in primary producers (Post, 2002) and hence inform about primary productivity.

In the intertidal, mussels and limpets are prominent suspension feeders and grazers, respectively (Bigatti and Penchasadze, 2008) and their shells often occur mixed with pinniped bones in hunter-gatherers shell middens (Gómez Otero, 2006, 2007; Orquera et al., 2011), Hence, the δ15N in the protein of the shell of rubbered mussels (Aulacoma atra atra) and limpets (Nacella magellanica) collected along the coast of Argentina has been measured in order to evaluate the correlation with the marine productivity of the water where they live. Once the correlation was confirmed the δ15N values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity and have been compared to the patterns of marine resource exploitation reported by previous zooarchaeological researchers (Yesner et al., 2003; Gómez Otero, 2006; Moreno, 2008; Favier Dubois et al., 2009; Tivoli and Zangrando, 2011). In this way, the hypothesis that the changing patterns of marine resource exploitation by hunter-gatherers along the south-western Atlantic coast of Argentina were driven by a bottom-up process and not by overexploitation was tested.

2. Methods
2.1. Study area and sampling

Modern mollusc samples (n ≥ 5 for each species) were collected from December 2009 to February 2010 at six sites along the coastline of Argentina: two in Rio Negro province (41°120′–43°38.40′; 64°10.80′–65°1.20′W), three in Santa Cruz province (47°44.40′–50°6.60′S; 65°50.40′–68°27.00′W) and one in Tierra del Fuego province (54°49.20′; 68°12.00′W) (Fig. 1). The limpet N. magellanica was collected in five sites, and the rubbered mussel A. atra atra was collected in four sites (see Table 1). As remotely sensed chlorophyll concentration can be used as an index of the mean water column chlorophyll (Smith, 1981), satellite data (SeaWIFS 9 km; http://reason.gsfc.nasa.gov/Giovanni) were used to determine current (January 2005 to January 2010) average

<table>
<thead>
<tr>
<th>Table 1</th>
<th>δ15N mean values (with standard deviation) of modern shells of the limpets and rubbered mussels collected along the coast of Argentina. The last column represents the chlorophyll-a levels mean values (with standard deviation) in each sample site.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>Province</td>
</tr>
<tr>
<td>Nacella magellanica</td>
<td>Rio Negro</td>
</tr>
<tr>
<td>Nacella magellanica</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Nacella magellanica</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Nacella magellanica</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Nacella magellanica</td>
<td>Tierra del Fuego</td>
</tr>
<tr>
<td>Aulacoma atra atra</td>
<td>Rio Negro</td>
</tr>
<tr>
<td>Aulacoma atra atra</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Aulacoma atra atra</td>
<td>Santa Cruz</td>
</tr>
<tr>
<td>Aulacoma atra atra</td>
<td>Tierra del Fuego</td>
</tr>
</tbody>
</table>

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chlorophyll-a levels in each sampling area. Chlorophyll-a is an index of the primary productivity in the oceans (Lorenzen, 1970).

Archaeological shell samples selected for isotopic analysis come from previous fieldwork carried out by authors Julieta Gómez Otero in Golfo San Matías and Peninsula Valdés (northern Patagonia) and Ernesto Piana and colleagues (Luis Orquera and A. Francisco Zan.grando) in the Beagle Channel (Table 2). Samples size was five for each species, site, and midden layer where available (Table 3). The samples were dated in different laboratories and using different methods, in particular samples from northern Patagonia, where all dated samples were marine shells instead of charcoal. Radiocarbon ages were calibrated by the authors using the package Clam 2.2 (Blaauw, 2010) and the new curve for Southern Hemisphere ShCal13 (Hogg et al., 2013). Reservoir effects data for northern Patagonia region are emerging only recently, and they suggest variable differences between marine and terrestrial ages (Cordero et al., 2003; Favier Dubois, 2009). The regional marine reservoir effect of 266 ± 51 years was included in the calibration of the shell samples (Favier Dubois, 2009).

Table 2
Archaeological sites where shells were recovered. Radiocarbon and calibrated ages were reported.

<table>
<thead>
<tr>
<th>Area</th>
<th>Site</th>
<th>Material</th>
<th>Radiocarbon age (14C BP)</th>
<th>Calibrated age (14C cal BP ±1σ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Patagonia</td>
<td>Las Ollas conchero 1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Shells</td>
<td>610 ± 60</td>
<td>268–508 (85.8%)&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>640 ± 60</td>
<td>278–519 (92.1%)&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Northern Patagonia</td>
<td>Ecocentro Fogón 3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Shells</td>
<td>850 ± 150</td>
<td>281–798 (94.7%)&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Northern Patagonia</td>
<td>Playa Las Lisas 2 – Perfil 1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Shells</td>
<td>2140 ± 60</td>
<td>2098–2502 (90.1%)&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Northern Patagonia</td>
<td>Cracker 8 – Nivel 3&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Shells</td>
<td>5200 ± 70</td>
<td>5465–5733 (83.9%)&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
<tr>
<td>Beagle Channel</td>
<td>Túnel VII&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Charcoal</td>
<td>100 ± 45</td>
<td>221–264 (17.0%)&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>Beagle Channel</td>
<td>Shämackush X site&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Charcoal</td>
<td>500 ± 100</td>
<td>498–518 (95.0%)&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>Beagle Channel</td>
<td>Innawaia I (M/K)&lt;sup&gt;g&lt;/sup&gt;</td>
<td>Charcoal</td>
<td>5750 ± 170</td>
<td>6187–6936 (95.0%)&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5870 ± 150</td>
<td>6310–6989 (95.0%)&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>5949 ± 50</td>
<td>6631–6885 (93.8%)&lt;sup&gt;g&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Gómez Otero (2006).
<sup>b</sup> Piana et al. (1992).
<sup>c</sup> Orquera and Piana (1999).
<sup>d</sup> Calibration of radiocarbon ages was carried out by the authors with the program Clam 2.2 (Blaauw, 2010), using the ShCal13 curve (Hogg et al., 2013). The probability is indicated in brackets.

<sup>e</sup> the regional marine reservoir effect of 266 ± 51 years was included in the calibration of the shell samples (Favier Dubois, 2009).
was included in the calibration of the shell samples (Favier Dubois, 2009).

For the characterization of resource use pattern by hunter-gatherers inhabiting the Beagle Channel (Fig. 2), we relied on the collections from six middens excavated at two archaeological sites 40 km apart. One location was situated at Cambaceres Bay and included archaeofaunal samples from stratigraphic layers dated 6000 BP, 1500 BP and from the 19th century. The other middens were located at Estancia Remolino and include assemblages dated 4000 BP, 1000 BP and 500 BP. There were no significant differences concerning excavation methods, as the same procedures were followed (see Tivoli and Zangrando, 2011 and references therein for further detail about the sites, dating procedures and collections). The collections from seven middens scattered in Bajo de la Quinta, Barranco de los Concheros and between Bahía Final 1 and Saco Viejo (northern coast of San Matías gulf), dated between 3430 ± 43 and 450 ± 80 14C BP, and information about archaeological sites located in Península Valdés, were used to characterize the pattern of resource use by hunter-gatherers inhabiting northern Patagonia (Fig. 3) (Gómez Otero and Suárez, 1999; Gómez Otero, 2007; Orquera and Gómez Otero, 2007; Favier Dubois et al., 2009).

### 2.2. Analytical methods

Both the archaeological and the modern shell samples were polished with sandpaper and with a diamond wheel drill to remove impurities. Then, they were rinsed with distilled water, dried at 50 °C and ground into a fine powder by mortar and pestle. Dried

![Figure 2](image_url)

**Fig. 2.** δ15N values in the shell of limpets from the Beagle Channel during the last 6600 years, including modern samples. The background colour represents the relative abundance of pinnipeds for hunter-gatherers in the area. Vertical bars denote standard deviation (n = 5). a – Tivoli and Zangrando, 2011; b – Orquera and Piana, 1999; c – Yesner et al., 2003.

### Table 3

<table>
<thead>
<tr>
<th>Species</th>
<th>Province</th>
<th>Site</th>
<th>Calibrated age (14C cal BP ±1σ)</th>
<th>N</th>
<th>Mean δ15N (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nacella magellanic</td>
<td>Chubut</td>
<td>Ecocentro Fogón 3</td>
<td>281–798 (94.7%)</td>
<td>5</td>
<td>13.5 ± 0.8</td>
</tr>
<tr>
<td>Nacella magellanic</td>
<td>Chubut</td>
<td>Playas Las Lisas 2 – Concho 2</td>
<td>2089–2502 (90.1%)</td>
<td>5</td>
<td>15.7 ± 0.8</td>
</tr>
<tr>
<td>Nacella magellanic</td>
<td>Chubut</td>
<td>Cracker 8 – Nivel 3</td>
<td>5465–5773 (83.9%)</td>
<td>2</td>
<td>14.1 ± 0.8</td>
</tr>
<tr>
<td>Nacella magellanic</td>
<td>Tierra del Fuego</td>
<td>Túnel VII</td>
<td>221–264 (17.0%)</td>
<td>5</td>
<td>12.5 ± 0.8</td>
</tr>
<tr>
<td>Nacella magellanic</td>
<td>Tierra del Fuego</td>
<td>Shmakhush X site</td>
<td>498–518 (95.0%)</td>
<td>4</td>
<td>12.2 ± 0.8</td>
</tr>
<tr>
<td>Nacella magellanic</td>
<td>Tierra del Fuego</td>
<td>Imiwaia I (M/K)</td>
<td>6187–6936 (95.0%)</td>
<td>5</td>
<td>13.4 ± 0.8</td>
</tr>
<tr>
<td>Aulacomya atra atra</td>
<td>Chubut</td>
<td>Las Ollas conchero 1</td>
<td>268–508 (85.8%)</td>
<td>5</td>
<td>13.1 ± 0.8</td>
</tr>
<tr>
<td>Aulacomya atra atra</td>
<td>Chubut</td>
<td>Playa Las Lisas 2 – Perfil 1</td>
<td>1589–1921 (95.0%)</td>
<td>5</td>
<td>13.7 ± 0.8</td>
</tr>
<tr>
<td>Aulacomya atra atra</td>
<td>Chubut</td>
<td>Cracker 8 – Nivel 3</td>
<td>5465–5773 (83.9%)</td>
<td>5</td>
<td>14.1 ± 0.8</td>
</tr>
</tbody>
</table>
powdered samples and secondary reference standards (acetanilide, urea, USGS 40 (d15N = -4.6‰), USGS 34 (d15N = -1.7‰), IAEA N2 (d15N = +20.3‰), IAEA N1 (d15N = +0.4‰), IAEA 600 (d15N = 1.0‰), UCGEMA F (d15N = +4.6‰)) were weighed and analyzed in a continuous flow stable isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA Thermo Finnigan) coupled with an elemental analyzer. We also employed a CO2 absorbent for elemental analysis (CaO/NaOH) to avoid spectrometer saturation by the CaCO2, which constitutes over 90% of the shell. Secondary standards were calibrated with the nitrogen international standard, atmospheric N2. Samples were processed at Scientific and Technological Centers (CCiT) of the University of Barcelona.

Stable isotope values, expressed in delta (δ) notation, in which the relative variations of stable isotope ratios are expressed in permil (‰) deviations from predefined international standards, were calculated as:

\[ \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 10^3 \]

where X is 15N, Rsample is the heavy-to-light isotope ratio of the sample (15N/14N), and Rstandard is the heavy-to-light isotope ratio in reference standards certified by International Atomic Energy Agency (IAEA, Vienna).

2.3. Statistical methods

Normality in data distribution was tested using the Lilliefors test and homoscedasticity using the Levene test. A linear regression was performed to investigate the correlation between modern shell δ15N with chlorophyll-a. ANOVA was used for multiple comparisons when data fit the normality and homoscedasticity requirements and the non-parametrical Kruskal–Wallis test was used otherwise.

The percentage of the number of specimens identified at the species level (%NISP) in the collections from the Beagle Channel (Tivoli and Zangrando, 2011) was used to calculate the relative abundance of otariids. Bone preservation was worse at the archaeological sites from northern Patagonia and therefore numbers of specimens had not been assessed (Favier Dubois et al., 2009). As a consequence, the relative importance of otariids in the collections from that area was assessed by calculating the percentage of broad taxonomic groups represented by otariids (%BTG) in each collection. A single collection was analyzed from each zone (Beagle Channel and northern Patagonia) and age. All statistical analyses were conducted with the PASW Statistic 18 software package.

3. Results

As the correlation between modern shell δ15N with chlorophyll-a was significant for both species (rubbed mussels, adjusted r-squared = 0.340, n = 22, p = 0.003; limpets, adjusted r-squared = 0.764, n = 25, p < 0.001), the δ15N values of the organic matter from shells collected at hunter-gatherer shell middens have been used as reliable proxies of past marine primary productivity.

The δ15N values of rubbed mussel shells from hunter-gatherers shell middens from northern Patagonia were higher than those of modern samples from the same areas (Kruskal–Wallis test,
Pinnipeds were exploited by hunter-gatherers since the very beginning of coastal settlement at the Beagle Channel, approximately 6400 years ago (Orquera and Piana, 1999; Tivoli and Zangrando, 2011). However, the dietary importance of pinnipeds, mainly fur seals (A. australis), declined steadily through the Late Holocene and has been negligible since approximately 1500 years ago (Yesner et al., 2003; Tivoli and Zangrando, 2011), in parallel to the decline of the δ15N values of limpet shells. This conclusion should be improved by further data for the period between approximately 6000 and 500 years ago, where there are no δ15N data. It can be argued that western sealers decimated fur seals (A. australis) in Tierra de Fuego at the end of the 18th and beginning of the 19th century (Schiavini, 1993), and hence, impeded the ability of hunter-gatherers to resume former exploitation levels during the Little Ice Age, when δ15N slightly rose. However, the occurrence of fur seal bones in middens was already extremely low 500 years ago, when the marine productivity had already decreased and European explorers had just reached the region.

The pattern of pinniped exploitation in northern and central Patagonia is more complex, as hunter-gatherers began the use of marine resources 7000 years ago (Orquera and Gómez Otero, 2007) but only intensified the exploitation of pinnipeds approximately 3000 years ago in Golfo San Matías (Favier Dubois et al., 2009), when the δ15N values in mollusk shells increased. The intensity of pinniped exploitation in Golfo San Matías declined approximately 1500 years ago (Gómez Otero and Suárez, 1999). The δ15N values of the rubbed mussels are also consistent with this pattern, although differences among Holococan samples were not statistically significant. Finally, coastal areas were abandoned following the domestication of feral horses of European origin at the beginning of the 18th century (Gómez Otero, 2006; Favier Dubois et al., 2009).

In conclusion, the overall evidence suggests that intense exploitation of pinnipeds by hunter-gatherers inhabiting the coastline of the Southwest Atlantic Ocean began when marine primary productivity was high and declined when marine primary productivity decreased. Accordingly, changes in the relative abundance of pinnipeds in the zooarchaeological record more likely reflect a bottom-up control of pinniped populations by marine primary productivity rather than overexploitation by hunter-gatherers. These findings indicate that hunter-gatherers along the south-western Atlantic coast of Argentina did not have a critical role in pinniped population declines, as in other coastal areas of New Zealand and northern Pacific (Anderson, 2008). This is a major advancement in the archaeology of the Patagonia and revealed that, despite the different mechanisms of livelihood observed in local populations, they had only a minor impact on pinnipeds. In contrast, the prolonged hunt by European sealers was the sole cause of their near extinction in the twentieth century.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quaint.2014.05.015.

References


